



## HIBERNATION

# Climate change is altering the physiology and phenology of an arctic hibernator

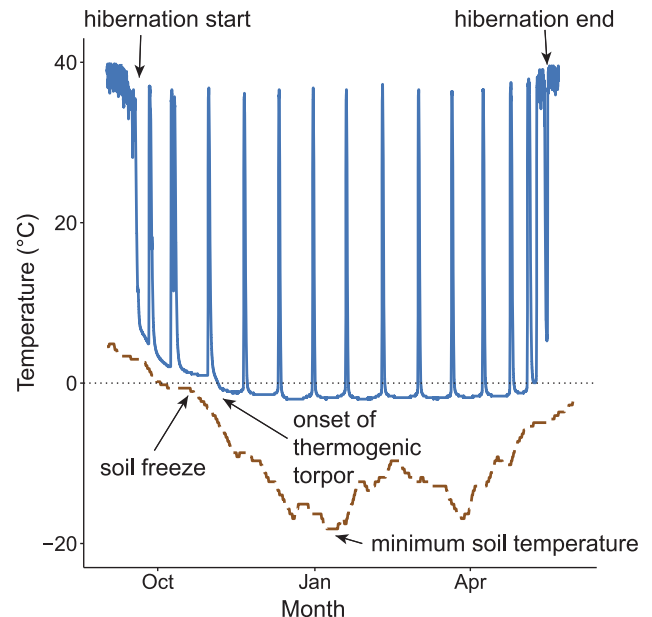
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Climate warming is rapid in the Arctic, yet impacts to biological systems are unclear because few long-term studies linking biophysiological processes with environmental conditions exist for this data-poor region. In our study spanning 25 years in the Alaskan Arctic, we demonstrate that climate change is affecting the timing of freeze-thaw cycles in the active layer of permafrost soils and altering the physiology of arctic ground squirrels (*Urocitellus parryii*). Soil freeze has been delayed and, in response, arctic ground squirrels have delayed when they up-regulate heat production during torpor to prevent freezing. Further, the termination of hibernation in spring has advanced 4 days per decade in females but not males. Continued warming and phenological shifts will alter hibernation energetics, change the seasonal availability of this important prey species, and potentially disrupt intraspecific interactions.

Climate change is particularly rapid in the Arctic (1), where systematic warming is reducing sea ice extent, altering hydrological cycles, thawing permafrost, increasing shrubs, and changing the timing of key seasonal events (phenological shifts) (2). Despite the rapid pace of climate change in the Arctic, it is a relatively data-poor region (3), and few long-term records combining physical records of climate change and physiological responses of organisms exist [but see (4, 5)]. Further, although changes in the spring and summer have received considerable attention, recent work has called for more research into the consequences of warmer and wetter winters (6). Winter conditions shape life histories, because many animal species have evolved strategies such as seasonal migration or dormancy to cope with prolonged periods of low food availability (7). In resident species that hibernate, climate change could lead to changes in energy expenditure and overwinter survival. Energy requirements increase markedly when hibernacula temperatures drop below an animal's thermal set point [near freezing for ground squirrels (8)], because animals must produce heat to prevent tissue damage and death (9). Winter temperatures may also contribute to the regulation of spring life history events (10, 11), and phenological shifts can have important ecological repercussions if they result in mismatches such that historically synchronous interactions within or among species are no longer temporally aligned (12, 13).

As part of a 25-year field study of arctic ground squirrels (*Urocitellus parryii*) in the Alaskan Arctic, we evaluated the impacts of climate change on this high-latitude mammalian hibernator, focusing on changes in hibernation physiology and emergence phenology. Unlike hibernators in most temperate or montane regions, which sequester themselves in hibernacula that remain above freezing, arctic ground squirrels overwintering in frozen soils must defend themselves against large thermal gradients (or differences between ambient and body temperatures) while torpid using nonshivering thermogenesis (thermogenic torpor) (9, 14) (Fig. 1). We demonstrate that significant warming in ambient air and soil (hibernacula) temperatures is altering hibernation phenology and the duration of thermogenic torpor in this arctic species.

**Fig. 1. Seasonal changes in arctic ground squirrel body temperature and soil temperature of the hibernaculum.** Abdominal body temperature of a hibernating arctic ground squirrel (blue line) and temperature of the surrounding hibernaculum (soil temperature at 1-m depth adjacent to the burrow entrance, dashed brown line) from a site near Toolik Field Station. Squirrels expend energy to maintain their body temperature above that of the hibernaculum ("thermogenic torpor") such that their brain temperatures never drop below 0°C (9).



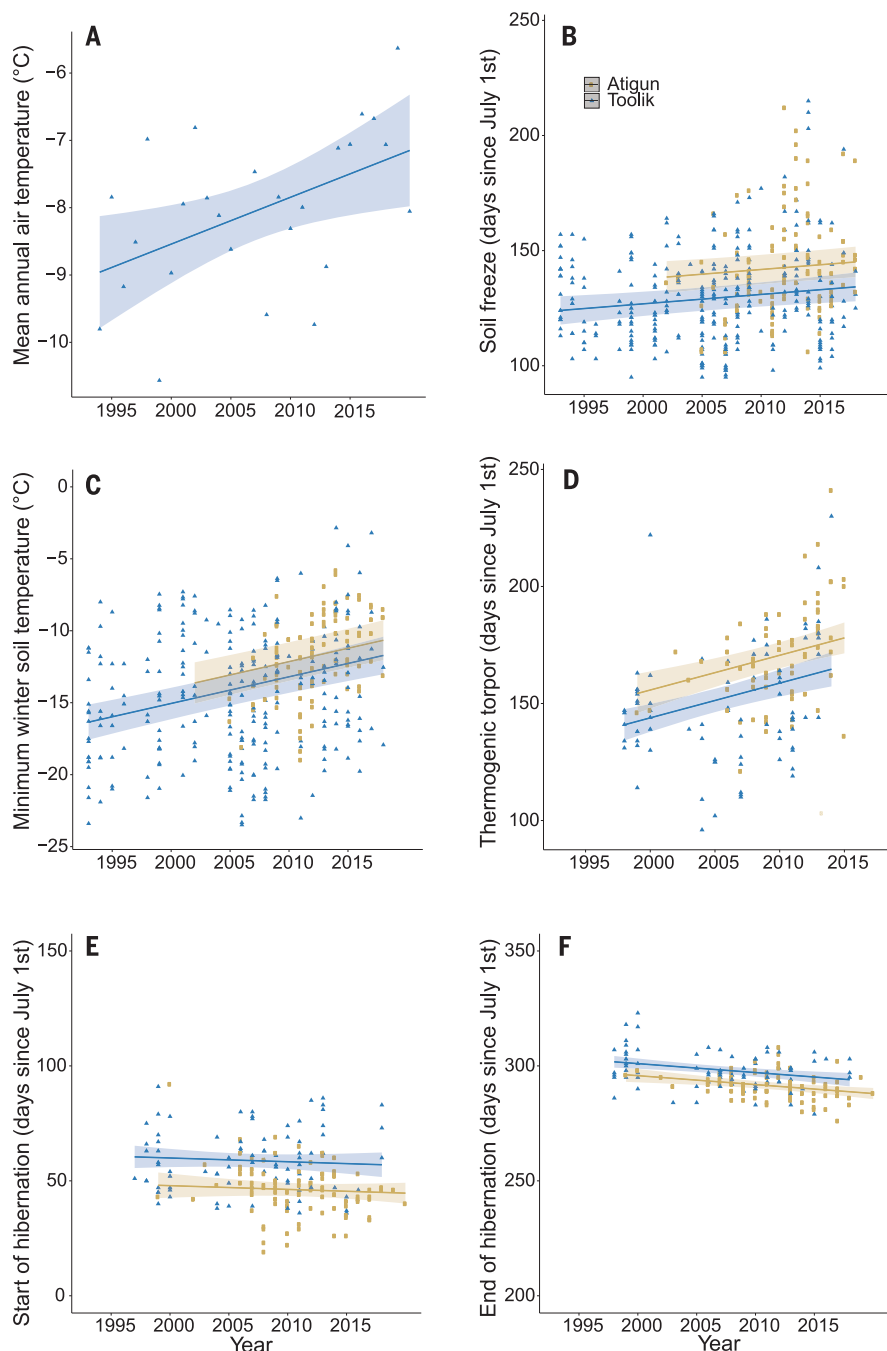
## Climate-driven changes in soil conditions alter hibernation

We used long-term climate records of air and soil temperature from two field sites, Toolik (68°38' N, 149°38' W; elevation 719 m) and Atigun (68°27' N, 149°21' W; elevation 812 m), in the Alaskan Arctic to document recent environmental change. The dataset durations were as follows: air temperatures at Toolik were measured from fall 1993 to spring 2020, Toolik soil temperatures from fall 1993 to spring 2019, and Atigun soil temperatures from fall 2002 to spring 2019. These measures were paired with hibernation records collected using biologgers (Toolik, fall 1996 to spring 2019; Atigun, fall 1999 to spring 2021) (15) to evaluate the physiological impact of recent climate change on arctic ground squirrels (see the supplementary materials). The use of biologgers that measured abdominal and/or skin temperature allowed us to record detailed information about physiological and phenological events during hibernation (Fig. 1, fig. S1, and table S1) from 199 free-living arctic ground squirrel individuals over 25 years.

Average annual air temperatures increased from 1994 to 2020 ( $\beta = 0.070$ ,  $t = 2.552$ ,  $P = 0.02$ ; Fig. 2A). This was driven by increases in winter temperatures, because seasonal analyses revealed increases in winter temperatures ( $\beta = 0.119$ ,  $t = 2.375$ ,  $P = 0.025$ ; fig. S2), but no annual trends for spring, summer, or fall (see the supplementary materials and fig. S2). Dates of soil freeze, measured at 1-m depth adjacent to hibernacula, shifted to be ~4 days/decade later in the fall ( $n = 446$ ,  $\beta = 0.409$ ,  $t = 2.851$ ,  $df = 383$ ,  $P = 0.0045$ ; Fig. 2B), and minimum soil temperatures in winter increased by almost 2°C/decade ( $n = 366$ ,  $\beta = 0.185$ ,  $t = 6.922$ ,  $P < 0.001$ ; Fig. 2C). Further, dates of soil thaw in summer advanced by ~0.3 days/decade

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**Fig. 2. Long-term changes in temperature and hibernation physiology.** Over the past 25 years at Toolik Field Station in the Alaskan Arctic, mean annual air temperatures increased (A), soil freeze date occurred later (sampling at 1-m depth, adjacent to hibernacula) (B), and minimum overwinter soil temperatures increased (C). Concurrently, the onset of thermogenic torpor occurred later in the fall [(D); shown for females only]. Although the date at which female ground squirrels initiated hibernation in the fall did not change over time (E), the date that they ended hibernation in the spring became earlier (F). Lines represent mean results of linear mixed effects models, and shaded regions represent 95% confidence intervals of the mean. Points represent raw data, and colors represent study sites (Atigun or Toolik). For all animal data, data points are plotted against the year in which an individual initiated hibernation.

( $n = 262$ ,  $\beta = -0.36$ , 95% credible interval,  $-0.57$  to  $-0.15$ ). In combination, this resulted in an  $\sim 10$ -day reduction in the annual duration that soil was frozen at 1-m depth over the study period.

In arctic ground squirrels, the date on which core body temperatures first decreased below  $0^{\circ}\text{C}$  each hibernation season, i.e., the date when squirrels first became thermogenic during torpor (9), was delayed by  $\sim 15$  days per decade

over the 25-year course of our study ( $n = 256$ ,  $\beta = 1.484$ ,  $t = 4.800$ ,  $\text{df} = 91$ ,  $P < 0.001$ ; Fig. 2D), with no difference seen between sexes ( $\beta = 3.039$ ,  $t = 1.041$ ,  $\text{df} = 161$ ,  $P = 0.299$ ). However, other phenological events did not show the same pattern. Neither adult males ( $n = 122$ ,  $\beta = -0.354$ ,  $t = -1.454$ ,  $\text{df} = 32$ ,  $P = 0.156$ ) nor adult females ( $n = 182$ ,  $\beta = -0.163$ ,  $t = -0.819$ ,  $\text{df} = 71$ ,  $P = 0.416$ ; Fig. 2E) changed the date at which hibernation began in fall. Adult females, however, ended hibernation earlier in spring ( $n = 166$ ,  $\beta = -0.389$ ,  $t = -3.592$ ,  $\text{df} = 60$ ,  $P < 0.001$ ; Fig. 2F) at a rate of  $\sim 4$  days/decade. As females ended hibernation earlier over the 25-year period, animal mass measured during the first 2 weeks after emergence increased ( $n = 91$ ,  $\beta = 3.472$ , 95% credible interval 0.196 to 6.781; see the supplementary materials and fig. S3). Males did not shift spring phenology ( $n = 120$ ,  $\beta = -0.192$ ,  $t = -1.103$ ,  $\text{df} = 30$ ,  $P = 0.279$ ). No directional changes were observed in parturition timing ( $n = 91$ ,  $\beta = -0.003$ ,  $t = -1.343$ ,  $\text{df} = 28$ ,  $P = 0.190$ ).

## Discussion

Winter plays a fundamental role in determining species' range limits and local population dynamics (6, 16). We show that warming in the Alaskan Arctic has altered seasonal freeze-thaw dynamics of the soil active layer and thus the thermoregulatory patterns of arctic ground squirrels during hibernation. Delayed freeze of the soil active layer near hibernacula is delaying the onset of thermogenic torpor and presumably reducing energy expenditure and overwinter weight loss. Further, we found sex differences in phenological responses to climate change, with females advancing their spring active season by 10 days over 25 years and males showing no change.

Warmer winter conditions and the shortening of the hibernation season in females have the potential to affect the survival probability of free-living arctic ground squirrels. There are several general mechanisms through which this could occur, including changes in energetics and predation exposure. First, delaying thermogenic torpor will decrease the total amount of time that arctic ground squirrels spend defending body temperature during hibernation, which will reduce overwinter energy expenditures (9, 17) and increase spring mass in females, as we have demonstrated in this study. Additionally, changes in winter temperatures will alter the energetic costs of torpor bouts and episodic interbout arousals (8) that characterize hibernation in small mammals. Arctic ground squirrels spend most of the hibernation season generating heat to avoid freezing, unlike most hibernators in more moderate climates, which can safely thermoconform because the surrounding soil temperatures remain above freezing during torpor (18). Reduced intensity and/or duration of thermogenesis caused by warmer conditions would

allow arctic ground squirrels to conserve energy and potentially increase winter survival, particularly among vulnerable, energy-limited age classes such as juveniles (19, 20). Alternatively, warmer conditions associated with climate change could shorten the hibernation season and increase the number of days that arctic ground squirrels are active above ground, increasing mortality rates because of increased exposure to predators (21). Thus, the consequences of climate change for hibernators will likely be heterogeneous (22). Although our study focused on a system in which warmer air temperatures lead to warmer hibernacula temperatures and likely reduced energy expenditure, in other systems, climate change may reduce snow depth, which can decrease burrow temperatures and decrease energetic savings through hibernation (20).

We found sex differences in phenological flexibility, with female arctic ground squirrels, but not males, terminating hibernation earlier. Other studies suggest that female ground squirrels are less sensitive to the direct effects of temperature (23, 24) and instead are responsive to temperature-driven changes in spring snow cover conditions (25). Thus, female flexibility appears to allow them to match energetic demands with the environment, and we expect that earlier snowmelt will also correspond with earlier vegetation green-up (26). As winters continue to warm, sex differences in phenological shifts may lead to disrupted intersexual interactions. For example, during one extremely warm spring in eastern Canada, female Richardson's ground squirrels (*Urocitellus richardsonii*) became sexually receptive before most males were physiologically prepared to mate, resulting in a phenological mismatch between the sexes (27). In the short term, mismatches such as these could affect population reproductive rates, and over longer time scales, continued warming in the

Arctic may be a strong selective force resulting in evolutionary changes in male phenology.

The consequences of climate change may be direct, such as the changes in hibernation physiology and phenology that we report here, as well as indirect. If the population size and temporal availability of arctic ground squirrels above ground are altered by climate change, then this could have cascading indirect effects on diverse tundra predators. Understanding the impact of climate change on species such as the arctic ground squirrel will aid assessments of how arctic food webs will function in a rapidly warming world, and research linking physiology and phenology to demographic responses is an important component of understanding community responses to climate change.

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#### SUPPLEMENTARY MATERIALS

[science.org/doi/10.1126/science.adf5341](https://science.org/doi/10.1126/science.adf5341)  
Materials and Methods  
Supplementary Text  
Figs. S1 to S3  
Table S1  
References (29–39)  
MDAR Reproducibility Checklist

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